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THE HOST RANGE OF *ACONOPHORA COMPRESSA* WALKER (HOMOPTERA: MEMBRACIDAE): A POTENTIAL BIOLOGICAL CONTROL AGENT FOR *LANTANA CAMARA* L. (VERBENACEAE)

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Abstract.–The membracid *Aconophora compressa* Walker is endemic to the Neotropics where it is found on various species of *Lantana.* Host range tests were conducted to ascertain whether it would be safe to introduce and release this insect in Australia for the biological control of *Lantana camara,* a serious weed in many tropical and subtropical countries. These tests, conducted in both Mexico and Australia, indicated that *A. compressa* was narrowly stenophagous. In all tests *A. compressa* oviposited and immatures developed on *L. camara.* In one of three tests oviposition and nymphal development occurred on *Duranta repens* and in two tests oviposition but not nymphal development occurred on *Jacaranda* spp. Oviposition did not occur on 55 other plant species tested. Permission to release this treehopper was obtained, and it was released in Queensland in 1995.

Key Words: Lantana, biological control, treehopper, *Aconophora*

The woody shrub *Lantana camara* L. (family Verbenaceae; subfamily Verbenoideae) is one of the world's ten worst noxious weeds (Muniappan et al. 1992) and infests millions of hectares of grazing and cropping land in 47 countries (Holm et al. 1977). Its highly aggressive nature leads to its taking over rangeland (Perkins and Swezey 1924, Kleinschmidt and Johnson 1977, Cilliers and Neser 1991), particularly gullies and hillsides with rich soils. Some varieties are also poisonous to livestock (Everist 1974).

Lantana camara has long been a target for biological control because it is an introduced plant, it infests rangelands where it may not be economic to treat with herbicides or clear physically, and because herbicide programs have not been particularly effective. Over a period of nearly 100 years there has been a number of investigations (Perkins and Swezey 1924, Winder and Harley 1983) resulting in 32 insect species being released in various countries (Julien 1992); a number easily surpassing that for any other weed species. However, effective control has been achieved only in parts of Hawaii (Perkins and Swezey 1924, Harley 1974). The biological control achieved in Australia is considered only partially effective (Winder and Harley 1983) and more biological control agents are desired (Taylor 1989).

A survey of the insect fauna on *L. camara* and three closely related congeners in North America was recently conducted

Table 1. Known host plants of eight species of *Aconophora* most according to Dietrich and Dietz (1991). Hosts on which immatures have also been found are denoted with an asterisk.

Species	Hosts
A. mexicana Stål	Anacardiaceae, Fabaceae, *Guanabanus* sp.*, *Piper auritum*
A. elongatiformis Dietrich	*Baccharis* sp.*, Fabaceae, Piperaceae*
A. elongata Dietrich	Fabaceae
A. compressa	*Lantana camara,* L. urticifolia*, L. hispida, Lippia myrocephala*
A. laminata Fairmaire	*Theobroma cacao, Lupinus* sp., *Baccharis conferta, Tetracera* sp.*
A. albipennis Dietrich	*Juniperus* sp., *Solanum tuberosum*
A. robusta Dietrich	*Alchornea* sp.*, *Croton gossipifolius**
A. marginata Walker	*Gladiolus*

(Palmer and Pullen 1995) to find further biological control agents. One species targeted for further study in that investigation was the membracid *Aconophora compressa* Walker, which was found to be damaging plants around Cuernavaca, Mexico. This paper reports the studies into the treehopper's biology and host range that were conducted before it could be released in Australia.

Biology

The tribe Aconophorini (Homoptera: Membracidae) consists of three genera: *Aconophora* Fairmaire, *Calloconophora* Dietrich and *Guayaquila* Goding (Dietrich and Deitz 1991). All of the Aconophorini are gregarious and subsocial, that is females guard their egg-masses and usually remain with nymphal aggregations throughout their development (Dietrich and Deitz 1991). Females guarding eggs sometimes aggressively confront predators with buzzing wings and physical contact. When disturbed, aggregations of adults usually disperse explosively but usually reaggregate, often at the original site. Ant mutualism is associated with the genus *Guayaquila* but has been observed with no species of *Aconophora* (Dietrich and Deitz 1991).

Female *A. compressa* oviposit up to 65 eggs to form a single cluster on stems. These eggs are oviposited over a number of days in a white froth, which hardens when dry so that the egg mass increases in size over the period of deposition. The female remains with this egg mass and its resultant progeny for the rest of her life. The eggs, each approximately 1.2 × 0.4 mm, hatch 14–20 days after oviposition. Nymphal development takes 4–6 weeks and usually involves 5 instars. The nymphs remain in an aggregation close to the empty egg mass and their mother.

Host Range and Phenology

Aconophora compressa occurs from Colombia in South America, through Central America, to Mexico. Three specimens were collected in Arizona, USA in 1930 (Dietrich and Deitz 1991). As this is the only record of an Aconophorini occurring north of Mexico it may be regarded with some doubt. In all probability the northern end of its range is Sinaloa, Mexico, some 400 k south of the of the United States border. *Aconophora compressa* is therefore essentially Neotropical. Within Mexico it is more common in central and southern areas. In the recent survey (Palmer and Pullen 1995) it was found at Veracruz and Oaxaca but was most abundant around Cuernavaca in the state of Morelos.

Aconophora compressa is a multivoltine species found throughout the year. Populations increase throughout the growing season (June–December) and are greatest at the end of that time and in the ensuing three months. Damaging numbers may occur from November to February.

The genus *Aconophora* includes 13 species (Dietrich and Deitz 1991). Hosts for 8 of these species are known (Table 1). Most congeners are fairly polyphagous. Older host record data must be treated with caution because the genus was substantially revised (Dietrich and Deitz 1991). The concept of *A. compressa* in particular has been in confusion since Goding (1928) transferred it to the genus *Guayaquila* and synonomized it with *A. caliginosa* Walker and *G. maxima* Goding without examining the type species (Dietrich and Deitz 1991). *Aconophora compressa* has recently (Palmer and Pullen 1995) been collected from *L. camara, L. urticifolia, L. hirsuta* and also from *Lippia myrocephala.* It has also been collected from an unidentified shrub with densely pubescent bark (Dietrich and Deitz 1991).

Host Specificity

Materials and methods.—Three independent experiments were conducted to ascertain the host range of this insect. The first two were conducted at the University of Morelos, Cuernavaca, Mexico prior to the insect being imported into Australia. The third experiment was conducted within quarantine facilities at the Alan Fletcher Research Station, Brisbane.

Experiment 1: The host specificity was assessed using standard, gauze covered cages approximately 1 × 1 × 1 m in dimension. Two replications were conducted; one in January 1991 and the other in February 1991. In each replication one potted plant of eight species was selected and placed in the cage. Adult *A. compressa* from a laboratory colony (20–40) were then introduced into the cage and scattered about so that there was every chance that they would be exposed to all the plants in the cage.

The plants were examined approximately twice a week for at least five weeks. Each plant was examined and the number of adults, egg masses, and nymphs noted. Counts made between the 6th and 37th days were used to estimate the mean population of adults on each plant species. Counts made between the 16th and 37th days were used to estimate the mean number of egg masses on each plant species. Counts made between the 30th and 37th days were used to estimate the mean population of nymphs on each plant species.

Experiment 2: Two plants each of 12 species were selected in March 1991 for a large cage experiment. The selection included 6 species of Verbenaceae, with the remainder being from closely related families. All the plants were examined prior to their selection to ensure that they were in good condition and were free of *Aconophora.* They were then watered before being placed inside a 2 × 3 × 7 m walk-in cage situated on the grounds of the University of Morelos.

The plants were placed inside the cage in two rows; each row containing one plant of each of the 12 species. Within these rows the plants were randomly assigned a position which were equidistant so that no plant was shadowed by its neighbours.

Adult *Aconophora compressa* were collected from one large bush of *L. urticifolia* growing on the university grounds. The insects were collected either by hand or aspirator and placed in plastic vials; fifteen to each vial. One vial was placed at the base of each plant in the experiment so that a total of 360 insects were placed in the cage. The insects then made their own way out of the vial and onto the plant.

The test was assessed twice a week for approximately seven weeks, a time sufficient for the insect to develop through a generation on the test plants. Each plant was examined and the number of colonies, adults, egg masses, and presence of nymphs noted. Six counts taken between the 23rd and 40th day after the experiment commenced, when all stages of the insect were present on the plants, were used to calculate the mean populations of adults, egg masses and nymphs reported here.

Experiment 3: Adult choice tests were carried out using gauze covered cages approximately 90 × 90 × 90 cm. Three rep-

Table 2. A summary of the abundance of adults, egg masses and nymphs found on experimental plants in three experiments conducted to determine the host range of *A. compressa.*

Plant Species	Expt. No.	Mean No. of Adults	Mean No. of Egg Masses	Mean No. of Nymphs
Verbenaceae				
Verbenoideae				
Lantana camara L.	1	7.8	3.3	33.7
L. camara	2	3.9	2.2	24.9
L. camara	3	19.4	8.4	
Lantana montevidensis (K. Spreng.) Briq.	1	0.3	0.0	0.0
L. montevidensis	2	0.0	0.0	0.0
L. montevidensis	3	0.03	0.0	0.0
Verbena carolina L.	2	0.0	0.0	0.0
V. bonariensis L.	3	0.0	0.0	
Duranta repens L.	1	0.4	0.0	0.0
D. repens	2	10.6	2.4	4.5
D. repens var. *lorentzii*	3	0.0	0.0	
Phyla nodiflora (L.) Greene	3	0.03	0.0	
Stachytarpheta urticifolia (Salsb.) Sims	3	0.14	0.0	
Viticoidae				
Callicarpa pedunculata R. Br.	3	0.0	0.0	
Clerodendrum sp.	2	0.0	0.0	0.0
C. cunninghamii Benth.	3	0.0	0.0	
C. tomentosum (Venten.)	3	0.0	0.0	
Petraea volubilis L.	2	0.0	0.0	0.0
Faradaya splendida F. Muell.	3	0.0	0.0	
Gmelina leichhardtii (F. Muell.) Benth.	3	0.0	0.0	
Premna lignum-vitae (Cunn. ex Shauer) Pieper	3	0.0	0.0	
Vitex trifolia L.	3	0.0	0.0	
Caryopteridoideae				
Glossocarya hemiderma (F. Muell. ex Benth.)	3	0.0	0.0	
Annonaceae				
Annona × *squamosa* L.	3	0.0	0.0	
Asteraceae				
Baccharis halimifolia L.	3	0.33	0.0	
Avicenniaceae				
Avicennia marina (Forssk.) var *australasica*	3	0.0	0.0	
Bignoniaceae				
Jacaranda sp.	1	0.3	0.0	0.0
Jacaranda sp.	2	1.1	0.3	0.0
Jacaranda acutifolia Humb. & Bonpl.	3	3.1	0.3	
Pandorea pandorana (Andr.) Steenis	3	0.0	0.0	
Boraginaceae				
Cordia dichromata G. Forster	3	0.0	0.0	
Ehretia acuminata R. Br.	3	0.03	0.0	
Chloanthaceae				
Chloanthes parviflora Walp.	3	0.0		
Spartothamnela juncea (Cunn. ex Walp.) Briq.	3	0.0	0.0	
Convolvulaceae				
Evolvulus alsinoides (L.) L.	3	0.0	0.0	
Ipomoea batatas (L.) Lam.	3	0.0	0.0	

Table 2. Continued.

Plant Species	Expt. No.	Mean No. of Adults	Mean No. of Egg Masses	Mean No. of Nymphs
I. plebeia R. Br.	3	0.03	0.0	
Polymeria calycina R. Br.	3	0.0	0.0	
Dilleniaceae				
Hibbertia scandens (Willd.) Dryand.	3	0.0	0.0	
Euphorbiaceae				
Croton insularis Baillon	3	0.0	0.0	
Ericaceae				
Azalea sp.	2	0.0	0.0	0.0
Lamiaceae				
Ajuga australis R. Br.	3	0.0	0.0	
A. cf. *reptans* L.	1	0.0	0.0	0.0
Ocimum basilicum L.	1	0.0	0.0	0.0
Lavendula dentata L.	3	0.0	0.0	
Plectranthus argentatus S. T. Blake	3	0.0	0.0	
Prosthantera ovalifolia R. Br.	3	0.0	0.0	
Mentha sp.	1	0.0	0.0	0.0
M. spicata L.	3	0.0	0.0	
Salvia splendens F. Sellow ex Roem. & Scult.	2	0.0	0.0	0.0
S. coccinea Juss. ex J. Murr.	3	0.03	0.0	
Scutellaria formosana N. E. Br.	3	0.0	0.0	
Teucrium argutum R. Br.	3	0.0	0.0	
Westringia fruticosa (Willd.) Druce	3	0.23	0.0	
Mimosaceae				
Acacia podalyriifolia G. Don	3	0.18	0.0	
Acacia concurrens Pedley	3	0.0	0.0	
Malvaceae				
Hibiscus rosa-sinensis L.	2	0.0	0.0	0.0
Myoporaceae	2	0.0	0.0	0.0
Myoporum parvifolium R. Br.	3	0.04	0.0	
Myrtaceae				
Eucalyptus crebra F. Muell.	3	0.0	0.0	
Eucalyptus curtisii Blakely & C. White	3	0.0	0.0	
Eucalyptus sp.	2	0.0	0.0	0.0
Pedaliaceae				
Sesamum indicum L.	3	0.0	0.0	
Piperaceae				
Piper novae-hollandiae Miq.	3	0.0	0.0	
Scrophulariaceae				
Duboisia myoporoides R. Br.	3	0.0	0.0	
Mazus pumilio R. Br.	3	0.0	0.0	
Solanaceae				
Cestrum nocturnum L.	1	0.2	0.0	0.0
Lycopersicon lycopersicum L.	3	0.0	0.0	
Solanum nemophilum F. Muell.	3	0.0	0.0	
S. pseudocapsicum L.	2	0.0	0.0	0.0
S. tuberosum L.	3	0.0	0.0	

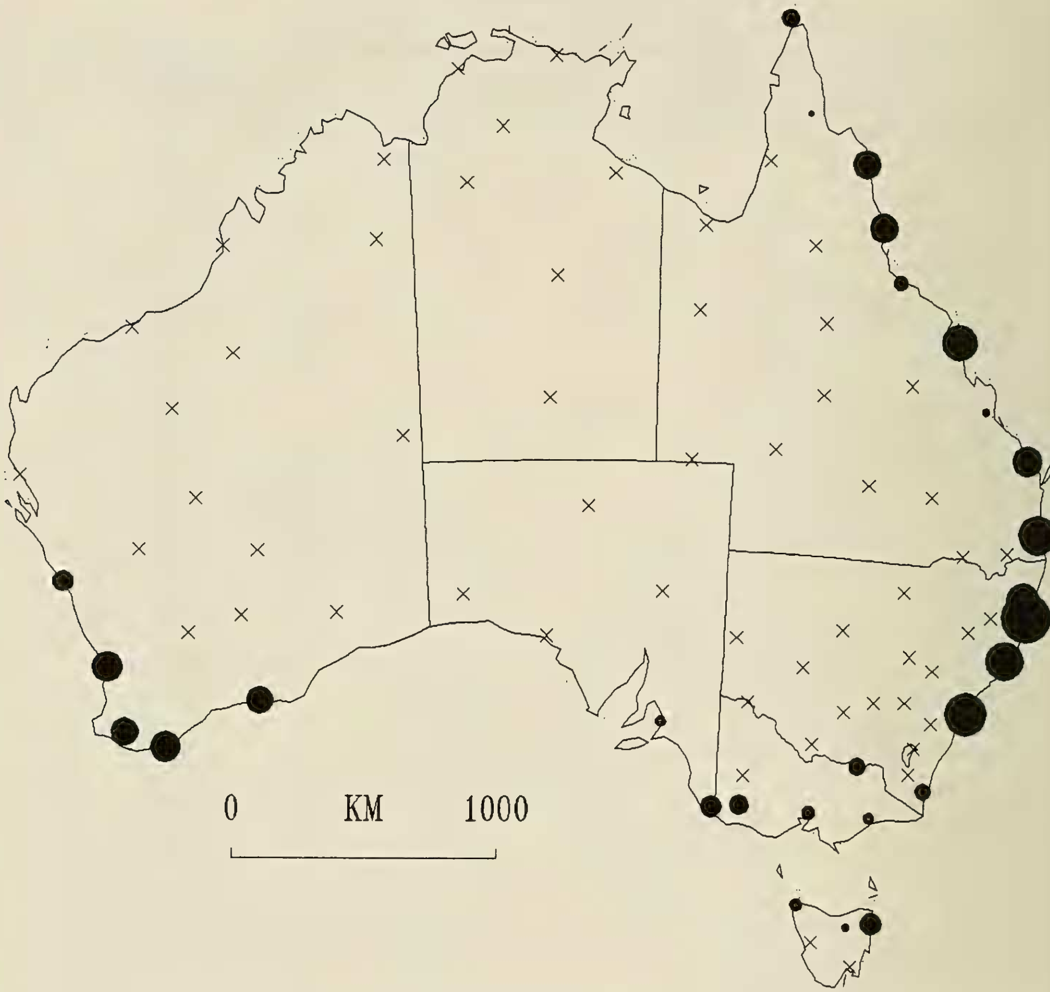

Fig. 1. Predicted distribution of *A. compressa* in Australia based on the climate matching model CLIMEX.

lications were conducted concurrently. In each replication, 9 plant species, always including *L. camara,* were arranged in a cage. Thirty adult *A. compressa* were then scattered into the cage. Counts of the adults on each plant were made between the 6th and 21st day after this introduction. Egg masses were counted on the 21st day.

Results.—The results of all three experiments are given in Table 2. *Lantana camara* was the only plant species on which *A. compressa* consistently oviposited. Oviposition also occurred on both plants of *Duranta repens* L. in one of three experiments and on *Jacaranda* spp. in all three experiments. The egg masses on *D. repens* produced nymphs that then developed normally on that host. Nymphs were never found associated with the egg masses on *Jacaranda* indicating that this plant is an unsuitable host.

Altogether this insect was tested against 62 plant species of which 17 were of the Verbenaceae and 13 and 5 species were of the closely related Lamiaceae and Solanaceae, respectively. The insect was in fact thoroughly tested along the centrifugal design advocated by Wapshere (1975). All evidence suggests that the host range of this insect is limited to *Lantana* and closely related genera such as *Duranta* and *Lippia.*

Release in Australia

Permission to release this insect in Australia was sought even though it could breed on Mexican varieties of *D. repens* (subfamily Verbenoidae). From an Australian perspective *D. repens* is an introduced ornamental suspected of being poisonous to children and stock (Everist 1974). The Verbenoidae is represented in Australia by one native species, *Verbena macrostachya,* which is found only in inland Queensland far from the habitat of *L. camara.*

Approval to release *A. compressa* was obtained in early 1995 and a mass rearing program outside the quarantine facilities was initiated. The climate matching model CLIMEX (Sutherst and Maywald 1985, Skarratt et al. 1995) was utilized in the selection of release sites. The model indicated (Fig. 1) that *A. compressa* should adapt to conditions along the eastern seaboard of Australia where *L. camara* is a problem. Conditions in southern Queensland and northern New South Wales should be particularly favorable.

First releases were made near Brisbane in May 1995 and at Charters Towers in October 1995.

Discussion

We anticipate that *A. compressa* will be a useful biocontrol agent if it establishes successfully. In Mexico it is quite damaging especially when a plant is attacked by multiple colonies. One reason for optimism is that its action will be largely independent of leaf status. *Lantana* has the ability to drop its leaves when stressed and uses this mechanism to survive periods of drought, cold, insect attack and possibly herbicide application. This reduces the effect of insects that attack foliage.

With the notable exception of the Coccoidea, the Homoptera have not been greatly used in biological control of weeds (Julien 1992). The psyllid *Heteropsylla* sp., released against *Mimosa invisa* L., and the aphid *Aphis chloris* Koch, released against *Hypericum perforatum* L., are other examples of Sternorrhyncha listed by Julien (1992). The only instance, to our knowledge, of the Auchenorrhyncha being so used is that of *Stobaera concinna* (Stål) released for *Ambrosia artemisiifolia* (L.) and *Parthenium hysterophorus* L. (Julian 1992). The reasons why the Homoptera other than Coccoidea have been so eschewed include the perception that most are polyphagous, that many are vectors of plant diseases, that they may be a greater than normal risk in quarantine facilities, that they are difficult to ship, and that their effects on the plant are slight or difficult to define.

Apart from *A. compressa* being the first use of a membracid for biological control, its progress will be of interest because it feeds on stems externally. Endophagous species such as stem borers and gall formers are more commonly used but there are few examples of ectophagous stem utilizers.

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